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MATING OF BUTTERFLIES

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THE PURPOSE OF THIS PAPER is to present the results of my studies of mating of eleven species and to review previous work on mating. All aspects of mating are included, including courtship, change of mating behavior with age, the roles of vision and odor during courtship, female behavior to reject courting males, anatomical source of pheromones, prezygotic isolating mechanisms, copulating posture, behavior during copulation, duration of copulation, number of matings per male and per female, the fate of sperm from different matings of one female, and the adaptive significance of a sphragis and of multiple mating. A detailed review of wing and body movements during courtship, too lengthy for this report, will be published later. The seven species I studied are: *Parnassius phoebus*, *Euchloe ausonides*, *Neominois ridingsi*, *Poladryas minuta*, *Precis coenia*, *Lycaena arota*, *L. xanthoides*, *Hypaurotis crysalus*, *Ochlodes snowi*, *Hesperia pahaska*, and *Amblyscirtes simius*. Details on these species will appear elsewhere. Perching behavior is defined as a mate-locating method in which males sit at characteristic sites and dart out at passing objects in search of females. Patrolling is a mate-locating method in which males fly almost constantly in search of females.

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Courtship (as distinct from copulation)

There is a tremendous diversity of courtship behavior. In patrolling species, the two sexes may meet during flight or the flying male may meet a female at rest. In perching species, the female flies near the male, who then pursues. Subsequent events can then be divided into aerial events and ground events although in some species identical activities may occur in the air and on the ground or plant. In the aerial phase, which is omitted altogether in some species and in courtships involving highly receptive females in other species, the two sexes often merely flutter about each other, or fly in stereotyped patterns, or one or both sexes may perform specialized acts for transferring pheromones. The aerial flight usually results in the female alighting, whereupon the receptive female usually becomes inactive until copulation occurs; successful matings with newly killed females have been obtained experimentally in *Euphydryas editha* and *Anthocaris charltonia* (Labine, 1966), *Hypolimnys misippus* (Stride, 1956), and *Argynnis paphia* (Magnus, 1950). Unreceptive females of some species may flap the wings or fly a special pattern (rejection dances), or may adopt a special rejection posture. After the female alights, the male may continue to fly about the female, or may land, whereupon one or both sexes may still flutter their wings, and the male may perform complicated maneuvers with his wings, antennae, or legs, etc. Copulation may then occur, or various courtship events may then be repeated. Courtships in different species may range from very simple with few events (*Parnassius*) to very complex (*Hipparchia semele*, Tinbergen et al. 1942; *Argynnis paphia*, Magnus, 1950). Little variation of the behavioral sequence occurs in successful courtship of some taxa (*Danaus*, Brower et al. 1965), but courtship may be quite variable in other taxa because various behaviors may be completely omitted, depending on the receptivity or age of the female (*Heliconius*, Crane, 1957; *Precis*; *Amblyscirtes*). Closely related species usually have similar courtship movements.

Courtship serves two functions: to promote mating between individuals of the same species and to prevent mating with other species. Because of the second function and the necessity of distinguishing mates from predators, individuals should be unreceptive toward the majority of animals in their habitat, and visual or olfactory characteristics that allow mutual recognition of the sexes will be selected for, even though these characteristics may have no other function. Courtship is probably a major

isolating mechanism in butterflies but isolating mechanisms have been poorly studied (see below). Most of the events during courtship have no useful function other than as token stimuli. In a few cases, however, behaviors seem to have some obvious function. The hairpencilling of *Danaus* (Brower et al. 1965), upward flight of *Argynnis* (Magnus, 1950), and bowing of *Hipparchia semele* (Tinbergen et al. 1942), all serve to place the male scent organs next to the female antennae, and wing fluttering of males of many other species serves the same function. Likewise, exposure of female hairpencils in *Heliconius* (Crane, 1957), and female glands in *Gonepteryx* (Lederer, 1938a), etc., serves the same function. Dropping of male *Danaus* onto some females makes them fly so that courtship can be repeated, usually with more success. "Male nudging" (male creeping under the wings next to the abdomen of the female, in various Nymphalidae) seems partly to make the female assume the copulatory position.

Sexual selection is important in butterflies, at least on males. Unreceptive females can sometimes be made to copulate after prolonged courtship by the male (*Ascia monuste*, Nielsen, 1961; *Aporia crataegi*, Stellwaag, 1924; *Pieris protodice*, Abbott, 1959; *Gonepteryx rhamni*, Lederer, 1938a; *Danaus gilippus*, Brower et al. 1965; *Precis coenia*, *Amblyscirtes*), which suggests that there is strong selection for males with persistent courtship or other behavioral, visual or olfactory attributes that increase female receptivity. Female butterflies almost never fly toward males to mate (except if she remains unmated for many days, see below), so that the only types of contacts in which copulation results are between receptive males and receptive or mildly unreceptive females. This places selective pressure on the male to develop sexual characteristics to make the unreceptive females receptive, because females do not have to make unreceptive males receptive. This may explain why males have brighter colors, in addition to their more active role in courtship. Also, sexual selection is stronger on the male because there is greater variance in number of matings per male than in number of matings per female and because females generally live longer (see below). The only selective pressures on the female are to inform the male of the specific identity of the female, and the various rejection behaviors described below are also of value to both sexes as they repulse a male which would otherwise harass the female for some time. Rejection dances

TABLE 1. Minimum age of mating.

Males

*Can mate on the first day of adult life**Poladryas minuta arachne*; Scott, this study*Phalanta phalanta*; Phipps, 1968*Chlosyne lacinia*; Drummond et al., 1970*Pieris brassicae* (mates most frequently the fifth day); David & Gardiner, 1961*Must mature several days before mating**Precis coenia* must mature at least a day before mating; Scott, this study*Euphydryas editha* must mature a day; Drummond et al., 1970*Cercyonis* spp. must mature a day, Drummond et al., 1970*Anthocharis* spp. take 1-2 days before mating; Lederer, 1941*Colias* spp. take 1-4 days before mating; Lederer, 1941*Hypolimnys misippus* do not court readily until the third day; Stride, 1956*Argynnis paphia* males start to patrol about the 2nd or 3rd day, so do not mate until then; Magnus, 1950*Heliconius erato* do not mate until the 3rd to 5th day; Crane, 1955*Limenitis* spp. do not mate until the 5th day; Platt, 1969

Females

*Can mate on the first day**Parnassius phoebus*; Scott, this study*Papilio rutulus*; Scott, this study*Anthocharis* spp.; Lederer, 1941*Pieris protodice*; Shapiro, 1970*Pieris rapae* (mate most readily the second day); Shapiro, 1970*Pieris brassicae* (mate most readily on fifth day); David & Gardiner, 1961*Eurema nicippe*; O. Shields & Emmel, 1973*Colias eurytheme*; Stern & Smith, 1960*Colias* spp.; Lederer, 1941*Ascia monuste*; Nielsen, 1961*Acraea* spp.; Marshall, 1901*Cercyonis* spp.; Drummond et al., 1970*Heliconius erato*; L. Gilbert, photograph*Heliconius charitonius*; Edwards, 1881*Phalanta phalanta*; Phipps, 1968*Hypolimnys misippus*; Stride, 1956*Anartia fatima*; Emmel, 1972*Limenitis* spp. (females mate most readily a day or two after emergence, but can mate after more than two weeks); Platt, 1969*Oeneis jutta*; Masters & Sorensen, 1969*Euphydryas editha*; Labine, 1966*Poladryas minuta*; Scott, this study*Must mature 1-2 days before mating**Chlosyne lacinia*; Drummond et al., 1970

may be subject to both individual selection on females and group selection on populations, because courtship of a highly unreceptive female wastes the male's time also.

Change of mating behavior with age

1) *Minimum age of mating* (Table 1) is earlier in females than in males. Females can mate the first day of adult life in almost all species, although females may mate more readily after a day or two. In contrast, males usually mate only after several days. Males often develop distinctive odors (male pheromones) only after a few days (Clark, 1926; *Papilio zelicaon*, Shields, 1967). Females of perching species often must fly to the mating sites, so may be older than patrolling species at first mating. The difference between the sexes in minimum age of mating is due to three reasons. Males almost always take the active role in mate-finding, so must be capable of stronger flight so must wait a few days before actively perching or patrolling. Second, it is advantageous to fertilize the females as soon as possible in the usual precopulation period so that the time for oviposition is not reduced. Finally, males almost always emerge a few days before females. In laboratory emergence, males emerge a day earlier in *Precis coenia*, one to two days earlier in *Pieris brassicae* (Roer, 1959), *Boloria toddi* and *Phyciodes tharos* (Oliver, 1972), and *Colias eurytheme* (Stern and Smith, 1960), and there are dozens of literature references to males predominating in the early part of the flight period and females more abundant later. Early emergence of males has no significance in continuously emerging species.

2) *Change of courtship with age*. In males, courtship behavior stays the same with age, but in females the behavior may change. Females on the first day may remain motionless, and the male may then join with few preliminaries, whereas older females may take a more active role. This is probably true in the patrolling species in which matings occur before the female's wings are expanded (see below), and in others. In *Heliconius*, one day old females eliminate all movements, and elicit almost no precopulatory behavior from males probably because of the greater strength of the pheromone when young (it is very strong in the pupa). Full courtship occurs only on the second or third days, and older females show progressively fewer responses. In *Colias*, wing movements of newly emerged females are limited in comparison with those of older females. In several species older mated females that are not seeking

mates fly after other individuals of both sexes, becoming more "masculine" in behavior (*Pieris rapae*, Priddle, 1960; *Heliconius*, Crane, 1955).

If a female remains unmated for many days, she flies toward passing males to seek a mate (*Parnassius phoebus*; *Heliconius*, Crane, 1955; *Hypolimnas*, Stride, 1956; *Danaus chrysippus*, Stride, 1958b), a behavior not shown by younger virgin females. In the perching species in which females fly to the mating sites after emergence, they merely fly about the mating site but do not approach males like the above species.

Role of vision in courtship. Experiments with models show that movement, size, and general color are important in courtship. Super-optimal models that flutter faster or are larger or have brighter colors than normal can be constructed in at least some species. The meeting of male and female involves the initial approach, and then the pursuing response of the male. In perching species (designated hereafter by the letter "P"), the initial approach is based principally on the movement and size of the female, while color and pheromones are more important later. In many patrolling species (designated hereafter by the letter "A") males often find sitting females, so that movement is probably less used, while color and pheromones are important both for the initial approach and later. This suggests that females of patrolling species should have brighter or more distinctive colors than females of perching species; this trend may be shown in the future when more species have been behaviorally classified. Most of the previous work has involved characteristics of the female. More work is needed on the use of male characteristics in courtship; many male butterflies are more colorful than the female, suggesting that male color may be more important in courtship than female color (or it may help males to recognize each other?). On the other hand, since the male is usually behind the female during courtship, male color would seem less important. Many polymorphisms in butterflies are limited to females, especially those involved in mimicry; perhaps sexual selection is paramount in males and selection to minimize predation more important in females.

Fluttering of the female is important for the approach of male *Hipparchia semele* (P, Tinbergen et al. 1942), *Argynnis paphia* (A, Magnus, 1954), *Limenitis camilla* (P, Lederer, 1960), and *Poladryas*, and probably many others, except that in most patrolling species males can approach and court resting females.

In perching *Poladryas*, tethered females do not attract males unless they flutter. In *A. paphia* models were more attractive to males the more rapidly they were fluttered, up to the flicker fusion frequency of the male eye. In *Heliconius*, male fluttering contributes to courtship success visually as well as olfactorily by disseminating androconial scales.

In *Hipparchia semele*, *Argynnis paphia*, and *Papilio rutulus* (A, Brower 1959), size of the female model is important for the initial approach in that models larger than the normal female produce more male responses (are supernormal). In *Hypolimnna misippus* (P, Stride, 1957), size is not important if the female model is not too large or too small. In *Precis* (P) and *Amblyscirtes* (P), males sometimes mate with crippled females whose wings are not normal size, and in many patrolling species males can mate with females whose wings are not yet expanded, so that the presence of superoptimal size either is not general or is not very important.

Shape of the female model was shown not to be important in *H. semele* (Tinbergen et al. 1942) and *A. paphia* (Magnus, 1954), and was of little importance in *Hypolimnna* (Stride, 1956), in which models with four wings were more attractive than those with two (which could be due to size rather than shape.)

The normal color of the female has been shown to be more attractive than other colors in many species: *Pieris napi* (A, Petersen et al. 1952), *P. rapae* (A, Obara, 1970), *A. paphia* (A), *Papilio glaucus*-group (A, Brower, 1959), *Boloria euphrosyne* (A, Eltringham, 1919), *Hypolimnna*, *Hypaurotis crysalus* (A), *Liminitis camilla*, *Anthocaris sara* (A, Evans, 1952), *Poladryas* (P), *Precis*, *Parnassius* (A), *Neophasia terlooiti* (A, J. W. MacSwain, oral communication), *Morpho* (A), *Anartia fatima* (A, Emmel, 1972). In *Heliconius erato*, pure red models of the female were more attractive than the normal female which has a red patch on black wings (Crane, 1955). In *Hipparchia semele* all colors gave about the same approach response, except that black was slightly superoptimal and white drew only 63% as many responses as brown (Tinbergen et al. 1942). If the pursuing response had also been studied, the acceptable color range might have been narrowed. Many butterflies are dull brown like *Hipparchia*, and in these color may not be as important as in other species. Swihart (1967b) showed for six species that the neural mechanism selects the output from optical receptors to maximize stimulation by the normal wing color. The male

may use the female colors more if receptive females spread their wings in courtship, as does *Hypolimnias*. The black color of male *Hypolimnias* is important for recognition by the female, but the white patches serve only to deter other males (Stride, 1958b). Male *Precis* artificially colored black courted females normally, even though blackened females were not courted normally, suggesting that movement of the male is more important than color, since the male is behind the female and the female never views his upperside directly. White inhibits the courtship responses of many dark colored butterflies (Stride, 1958a).

When the wings are multicolored, the gross but not detailed pattern may be used in courtship. In *Limenitis camilla*, which has a broad white stripe on dark wings, models with the normal width, spacing, and pattern of the white bands are more attractive to the male than other models (Lederer, 1960). In *Hypolimnias*, the color of the female hindwings is more important in eliciting male response than frontwing color (Stride, 1956), and the black border of the female wings increases male response slightly (Stride, 1957). In *Anartia fatima*, the white band is most attractive to males but red spots slightly increase attractiveness (Emmel, 1972). The detailed pattern of lines and spots of the female is not used by males in the following species: the black spots of *Pieris rapae* (Obara, 1970); the dark lines of *Pieris napi* (Petersen et al. 1952); the dark veins and spots of *Argynnis paphia* (Magnus, 1958), the orange spots and black areas of *Hypaurotis*; and the individual eyespots of *Precis*.

Female behavior to reject males. Females of many species have special rejection behavior which visually causes the male to leave or to cease courtship for a moment. The following 8 behaviors have been observed. Numbers 1 and 2 can be called "rejection dances," and numbers 3 to 5 "rejection postures."

1) The female flies vertically until the male returns to the ground in *Poladryas* (unreceptive virgins may also flutter slightly), *Colias*, *Gonepteryx rhamni* (Lederer, 1938a), *Pieris rapae* (in all three the pierid rejection posture may also be used, or the female flies away), *Erynnis tristis* (Shields, 1967), *Hypolimnias* (mated females only, Stride, 1958b).

2) The female rapidly flaps her wings in *Hipparchia* (Tinbergen et al., 1942), *Chlosyne gorgone* and *C. nycteis*, *Precis coenia*, *Lycaena* spp., *Hesperia* spp., *Ochlodes snowi*, *Poladryas* (unreceptive virgins flutter slightly), *Euphydryas editha* (La-

bine, 1966), and *Hypolimnias* (mated females "quiver" like the male and fly upward).

3) The Pieridae rejection posture (abdomen vertical, wings horizontal) has been recorded in the following Pieridae and probably occurs in all: *Colias*, *Anthocaris* (Lederer, 1941; Temple, 1953), *Euchloe ausonides*, *Pieris rapae*, *Pieris brassicae* (David and Gardiner, 1961), *P. protodice* (Shapiro, 1970), *Aporia crataegi* (Stellwaag, 1924), *Gonepteryx rhamni*, and *Glutaphrissa saba* (the last two may have a repellent pheromone, See No. 8 below). *Heliconius erato* uses this posture to reject males, while other *Heliconius* spp. use the posture to attract males (Lawrence Gilbert, oral communication).

4) The unreceptive female spreads her wings in *Graphium podalirius* (Lederer, 1960).

5) Unreceptive virgin female *Hypolimnias* close the wings above the thorax when the male courts (the wings are spread during successful courtship), and the female flies away or drops to the ground if the male tries to copulate. Mated unreceptive female *Hypolimnias* also quiver like the male and fly upward; this species has the most complicated rejection behavior known in butterflies (Stride, 1958b).

6) Unreceptive females have no special rejection behavior and merely fly away in *Danaus gilippus* (Brower et al. 1965). *Nordmannia ilicis* (Fiori, 1957), *Neominois*, *Amblyscirtes*, *Hypaurotis* (or crawls away), *Parnassius*, *Limenitis camilla* (Lederer, 1960), *Papilio dardanus*, and *P. demodocus* (both Stride, 1958b). In *Parnassius* and *Limenitis* the female may close her wings when a male comes near as in number 5, but this seems to be to prevent recognition by the male. In species with special rejection behaviors the female may also merely fly away (*Colias*, *Pieris rapae*, *Hypolimnias*). *P. rapae* females may drop to the ground, and then do the Pieridae rejection posture.

7) Males do not follow mated older females apparently because of lack of pheromone production in *Agathymus* (Roever, 1964), *Parnassius*, and to some extent in *Euphydryas editha* (Labine, 1966) and *Precis*. Males turn away from mated *Argynnis paphia* after antennal contact (Magnus, 1963).

8) The female may have a repellent pheromone in *Gonepteryx rhamni* (Lederer, 1938a) and *Glutaphrissa saba* (Poulton, 1912) since both extrude the abdominal glands during the rejection posture and at least *Gonepteryx* does not extrude them during normal successful courtship. *Pieris* and *Euchloe* have complicated lobes on the end of the abdomen, which perhaps

emit a pheromone. In *Heliconius* females develop a strong odor an hour after mating which prevents further matings and which is apparently deposited by the male (Lawrence Gilbert, oral communication). A different pheromone is used before and during courtship (Crane, 1955). Males of *Heliconius erato* sitting on a female pupa, waiting for the virgin to emerge fly away when a mated female is brought near (Lawrence Gilbert, oral communication).

There is no apparent taxonomic correlation in the above rejection behaviors, except for the Pierid rejection posture. Most of the rejection behaviors above are not shown by the male, but in some cases the female rejection behavior mimics some behavior of males and so perhaps visually convinces the male he is courting another male: In *Poladryas*, *Erynnis*, and occasionally in *Colias*, the female flies up in the air which mimics the vertical encounters of two males. In *Precis*, females flutter, which imitates male courtship fluttering. In *Hypolimnias*, females may quiver like courting males, and females fly up in the air, which mimics vertical encounters which probably occur because it is a perching species. Males can sometimes overcome rejection behavior after prolonged courtship (see above).

Male behavior to reject males. Males have no reason to reject females but may need to reject other males. In laboratory cultures of *Pieris brassicae*, where a male could not escape the attentions of another male, sometimes resting males gave the female Pieridae rejection posture when courted by other males (David and Gardiner, 1961). In *Precis coenia*, a teneral male may flutter his wings like the female rejection dance when courted by another male. The color of male *Hypolimnias* deters other males (Stride, 1956), but this species is sexually dimorphic unlike most butterflies. The vertical encounters between males described previously under perching behavior are attempts to elicit female behavior rather than rejection behavior.

Role of pheromones in courtship. Pheromones of one or both sexes are important in courtship of most species although only in Danainae have pheromones been chemically identified. In all species except the few using a long-distance pheromone, the pheromone is used only within one to two meters. Female pheromone evokes the male pursuing response and causes continued courtship, while the male pheromones may cause the female to land and accept the male. In *Pieris rapae* (Obara, 1970), *Hypaurotis*, *Hypolimnias* (Stride, 1956), *Argynnis paphia* (Magnus, 1958), *Hipparchia semele* (Tinbergen et al. 1942),

Papilio glaucus-group (Brower, 1959), and probably most species vision is more important early in courtship and pheromones are more important in later stages. In *Hypolimnna*, substitution of a male for the female in the later stages of courtship does not stop courtship, indicating that the visual difference between the sexes used earlier has no effect at close range.

There is behavioral evidence for male pheromones in Danaeinae, *Hipparchia semele* (Tinbergen et al. 1942), *Argynnis paphia* (Magnus, 1950), *Erynnis tristis* (Shields, 1967), and *Ithomia heraldica* (Lawrence Gilbert, written communication), and *Colias philodice* (Orley Taylor, oral communication). Pheromones have been isolated in three species of Danaeinae, and their mode of action determined (see isolating mechanisms below). Longstaff (1912) and Clark (1926) found strong male odors of hundreds of species; often these odors develop only after a few days and are strong in older males. Perhaps 50% of all butterfly species have male structures which presumably emit pheromones (Table 2). The organs of males are setae modified into long hairs gathered into tufts, or setae modified into scales of various types, including long tapered scales with terminal tufts called "androconia". These modified setae are associated with glands. The location in males is usually on the wings (especially the upperside of the forewings), but occasionally on legs or abdomen, because males often flutter during courtship, and they are usually behind the female. The function of androconia in *Hipparchia semele* was shown by excising the part of the wing containing androconia; such males had great difficulty in acquiring a mate (Tinbergen et al. 1942). In *H. semele*, *Argynnis paphia*, and *Erynnis tristis*, the male brings the androconial areas of the wing next to the female antennae. However, all three of these species have close relatives which either do not do this, or have the same courtship pattern and lack androconia. Such cases of direct contact between androconia and antennae are unusual, and in most cases the androconia are necessarily transmitted via air currents from male to female. In males of most groups except Danaeinae, Ithomiinae, some Papilionidae, and probably other groups, male pheromone-organs occur in one species and are absent in closely related species in a seemingly random fashion; thus only 26 of 69 *Erebia* species possess androconia (Warren, 1936); and in Nearctic *Erynnis*, one species has the tibial hair tuft only, six species have tibial tuft and front wing costal fold, and nine species have only the costal fold (Burns, 1964). It can

TABLE 2. Anatomical source of pheromones (Dixey, 1932; Illig, 1902; Gotz, 1951; Barth, 1944, 1952, 1959, 1960; Urbahn, 1913; Freiling, 1909; Eltringham, 1912; Kames, 1966; Clark, 1926).

Male	Hair-pencils	Female
tibial tuft on hind leg fits into thoracic pouch in many Pyrginae abdomen, and gland on hind wing in <i>Acraea thalia</i> , <i>Danainae</i> abdomen of <i>Melete</i> , <i>Morpho</i> hindwing of <i>Ithomiinae</i> , <i>Typhe-danus</i> , <i>Mycalesis mineus</i>		abdomen in <i>Heliconiini</i> , <i>Gonepteryx rhamni</i> , <i>Glutaphrissa saba</i> , <i>Catopsilia</i> , <i>Melete</i> , <i>Papilio machaon</i>
Modified Scales		
abdomen of <i>Brassolini</i> hindwing of <i>Stichophthalma camadeva</i> , some <i>Papilioninae</i> (<i>Parides</i> , etc.) patches on forewing in many <i>Hesperiinae</i> fold on costa of forewing in many <i>Pyrginae</i> patches on both wings of many <i>Pieridae</i>		abdomen of <i>Euploea asela</i> underside of forewing in <i>Thymelicus lineola</i>
Androconial Scales		
scattered over wing in <i>Pieridae</i> , <i>Lycaenini</i> , <i>Plebejini</i> , <i>Erebia</i> small patch on front wing in many <i>Theclini</i> small patch on hind wing in some <i>Colias</i> large patch on front wing in many <i>Satyrinae</i> along veins of front wing in <i>Melitaeini</i> , <i>Argynnini</i> patches on both wings in many <i>Heliconius</i>		
Glands Not Associated With Modified Scales		
invaginated glands on abdomen in <i>Didonis</i> , <i>Argynnis</i> , <i>Heliconius</i>		external lobes near ovipositor in <i>Euchloe</i> , <i>Pieris</i> invaginated glands on abdomen in <i>Aglais urticae</i> , <i>Boloria</i> , <i>Argynnis</i> , <i>Vanessa</i> , <i>Didonis</i>

TABLE 3. Species for which female pheromones are suspected from behavioral evidence.

- Parnassius phoebus*, Scott, this study
Papilio glaucus-group, Brower, 1969; Scott, this study
Pieris napi, Petersen, 1952
Pieris protodice, Shapiro, 1970
Colias philodice, Stern & Smith, 1960
Gonepteryx rhamni, Lederer, 1938a
Glutaphrissa saba, Poulton, 1912
Oeneis jutta, Masters & Sorensen, 1969
Hipparchia semele, Tinbergen et al. 1942
Neominois ridingsii, Scott, this study
Euphydryas editha, Labine, 1966
Boloria sp., Eltringham, 1919
Coenonympha sp., Eltringham, 1919
Danaus gelippus, Brower et al. 1965
Heliconius erato (two pheromones), Crane, 1955; Lawrence Gilbert, oral communication
Heliconius charitonius, Edwards, 1881
Planema spp., Eltringham, 1912
Euphydryas anicia, Scott, this study
Argynnis paphia, Magnus, 1950
Chlosyne damoetus, Scott, this study
Precis coenia, Scott, this study
Hypolimnas misippus, Stride, 1956
Limenitis camilla, Lederer, 1960
Aglais urticae, Temple, 1953
Hypaurotis crysalus, Scott, this study
Glaucopsyche lygdamus, Scott, this study
Erynnis brizo, Burns, 1964
Hesperia pahaska, Scott, this study
Agathymus spp., Roever, 1964
Anthocharis, Lederer, 1941

TABLE 4. Sex which carries the other when a copulating pair is disturbed. *—both sexes have been recorded flying. Compiled from field observations by the present author (number of observations in parentheses); Lederer, 1938a, 1938b, 1941, Stellwaag, 1924; Rutkowski, 1971; Phipps, 1968; Crane, 1955; Tinbergen et al. 1942; Stride, 1956; Malicky, 1961; Poulton, 1918; Wheeler, 1915; McCubbin, 1971; L. E. Gilbert, oral communication; Shields & Emmel, 1973; and many references cited by the latter reference.

Male Flies

Pieridae: *Pieris rapae* (1), *P. beckeri*, *P. manni*, *P. sisymbri*, *P. occidentalis* (1), *P. brassicae*, *P. protodice* (2), *P. virginiensis*, *P. napi*, *P. doxo**, *Dixeia pigea*, *D. charina simana**, *Belenois gidica*, *B. creonia severina*, *B. mesentina*, *Appias drusilla*, *Herpaenia eriphia*, *Catasticta nimbece*, *Eurema lisa*, *E. desjardinsii regularis*, *E. brigitta*, *E. hecabe senegalensis*, *E. mexicana* (1), *E. nicippe*, *Anthocharis cethura*, *Colotis achine*, *C. evippe omphale*, *C. evagore*, *C. evenina casta*, *C. ducissa*, *Eronia cleodora*, *Catopsilia florella*, *Nathalis iole*, *Phoebus sennae* (1), *Pontia daplidice*, *Colias cesonja* (3), *C. edusa*, *C. hyale**, *C. philodice* (2), *C. eurytheme* (4), *C. palaeno*, *C. crocea**, *C. occidentalis*, *C. phicomone*, *Gonepteryx rhamni**, *Glycestha aurota*, *Pinacopteryx eriphia*

Nymphalidae, Danainae: *Danaus gilippus* (1), *D. plexippus*, *D. chrysippus*
Acraeinae: *Acraea caecilia*, *A. oncaea*, *A. caldarena**

Satyrinae: *Melanargia galathea**, *Maniola jurtina**, *Brintesia circe*, *Chazara briseis*

Nymphalinae, Heliconiini: *Heliconius erato* and many other *Heliconius* spp.

Argynniini: *Argynnis adippe**, *A. paphia**, *A. niobe**, *A. aglaja**, *A. atlantis* (4), *A. nokomis**, *A. lathonia**, *A. cybele**, *A. mormonia**, *Euptoieta claudia**

Boloria: *B. selene*

Melitaeini: *Melitaea diamina*, *Melicta athalia**

remaining Nymphalinae: *Biblia acheloia*, *B. goetzii*, *Anartia fatima*, *Phalanta phalanta*

Lycaenidae

Lycaeninae

Lycaenini: *Lycaena tityrus*, *L. arota**, *L. editha*, *L. subalpina*

Plebejini: *Cupido osiris*, *Syntarucus pirithous**, *Plebejus shasta**, *P. argyrognomon*, *P. argus*, *P. saepiolus** (1), *P. melissa** (1), *P. acmon** (2), *P. icarioides** (1), *Polyommatus icarus*, *P. eros*, *Plebicula escheri*, *P. dorylas*, *Meleageria daphnis*, *Lycaeides idas*, *Lysandra coridon*, *L. bellargus*, *Agríades glandon** (3), *A. thetis*, *Hemiargus isola** (2), *Glaucopsyche alexis*, *G. lygdamus* (2), *Everes alcetas*, *Agrodiaetus damon*, *Albulina orbitulus*, *Aricia agestis*, *Philotes baton*, *P. battoides**, *P. enoptes**, *P. rita*, *Leptotes marina**

Hesperiidae

Female Flies

Papilionidae

Parnassius apollo, *Zerynthia polyxena*, *Z. rumina*, *Battus philenor* (1), *Papilio bairdii*, *P. polyxenes*, *P. p. rudkini*, *P. machaon*, *P. zelicaon*, *P. dardanus*, *P. polytes*, *P. echerioides*, *P. jacksoni*, *P. alcinous*

Pieridae

*Pieris doxo**, *Pieris* spp. (seldom), *Gonepteryx rhamni** (usually), *Aporia*

crataegi (based on 15 pairs), *Eurema nise* (1), *Ascia monuste*, *Dixeia charina simana**, *Colias hyale**, *C. crocea**

Nymphalidae, Acraeinae

Acraea chilo, *A. encedon*, *A. natalica*, *A. caldarena**

Satyrinae

Pyronia cecilia, *P. tithonus*, *Satyrus actaea*, *S. cordule*, *Satyre justina*, *Coenonympha arcania*, *C. gardetta*, *C. pamphilus*, *C. tiphon*, *C. satyrion*, *C. tullia* (1), *Erebia albertanus*, *E. oeme*, *E. manto*, *E. euryale*, *E. aethiops*, *E. gorge*, *E. claudina*, *E. goante*, *E. stirius*, *E. montanus*, *E. medusa*, *Melanargia galathea**, *Maniola jurtina**, *M. tithonus*, *Lastommata megera*, *L. maera*, *Hipparchia neomiris*, *H. semele*, *Ypthima asterope*, *Euptychia cycla*, *E. hermes*, *Aphantopus hyperantus*, *Pararge hiera*, *P. aegeria*, *Pierella luna*, *P. helvina*, *Cercyonis pegala* (9), *C. oetus* (2), *C. meadi* (2), *Neominois ridingsii* (2), *Oeneis chryxus* (3), *O. taygete* (1), *O. melissa* (1), *Minois dryas*

Nymphalinae, Argynniini

*Argynnis adippe**, *A. paphia**, *A. niobe**, *A. aglaja**, *A. pandora*, *A. nokomis**, *A. cybele** (1), *A. aphrodite*, *A. idalia*, *A. callippe* (1), *A. egleis*, *A. hydaspe*, *A. mormonia**, *A. edwardsi* (1), *A. lathonia**, *Euptoieta claudia** (1)

Boloria

B. daphne, *B. euphrosyne*, *B. pales*, *B. titania*

Melitaeini

Euphydryas aurinia, *E. chalcadon*, *E. editha*, *Melitaea cinxia*, *M. helvetica*, *M. didyma*, *Mellicta athalia**, *Poladryas minuta arachne* (9), *Phyciodes orseis* (1), *P. campestris* (4), *P. mylitta*, *P. tharos*, *Chlosyne gorgone* (3), *C. leanira fulvia* (1), *C. lacinia* (2), *C. californica*, *C. damoetas malcolmi*, *C. gabbi*, *Mellicta asteria*, *M. varia*, *Microtia dymas*

remaining Nymphalinae

Asterocampa leilia, *Anartia jatrophae*, *Limenitis bredowi*, *Hamanumidia daedalus*, *Pseudocraea poggei*, *Neptis agatha*, *Precis actia*, *P. coenia* (22), *P. clelia*, *P. villida*, *Hypolimnys misippus*, *Apatura iris*

Lycaenidae, Riodininae

Apodemia mormo

Lycaeninae, Theclini

Alaena interposita, *Axiocerses amanga*, *Hypaurotis crysalus* (1), *Satyrium saepium* (1), *Harkenclenus titus*, *Nordmannia acaciae*, *N. ilicis*, *Strymonidia spini*, *Callophrys apama* (2)

Lycaenini

Lycaena hippothoe, *L. phlaeas*, *L. arota** (1), *L. helloides* (1)

Plebejini

Cupido minimus, *Syntarucus pirithous**, *Hemiargus isola** (1), *Plebejus icarioides** (1), *P. acmon** (1), *P. shasta**, *P. saepiolus** (1), *P. melissa** (1), *Agriades glandon** (1), *Maculinea arion*, *Cyaniris semiargus*, *Evers comyntas*, *Eumedonia eumedon*, *Leptotes marina**, *Philotes battoides**, *P. enoptes** (1)

Hesperiidae

Amblyscirtes simius (4), *Hesperia pahaska* (2), *H. juba*, *H. comma* (3), *H. ryffellensis*, *Thymelicus sylvestris*, *Polites coras*, *P. sonora*, *Adopaea thamas*, *Euphyes conspicua*, *Hylephila phyleus*, *Cartharodus lavatherae*, *Erynnis telemachus* (2), *E. tristis*, *E. persius* (2), *E. tages*, *E. brizo*, *E. funeralis*, *E. juvenalis*, *Polythrix asine*, *Cogia calchas*, *Atrytone conspicua*, *Ochlodes sylvanoides*, *O. venatus*, *Pholisora catullus*, *Pyrgus alveus*, *P. carlinae*, *P. communis*, *P. malvae*, *P. serratulae*, *Thorybes diversus*

TABLE 5. Duration of copulation (*mate only during part of day).

- Parnassius phoebus* average about 3 hr., rarely 24 hr.; Scott, this study; Edwards, 1868
- Parnassius* spp. 1-12 hr., rarely 48 hr.; Lederer, 1938b; Edwards, 1868
- Zerynthia* sp. 1 hr.; Lederer, 1938b
- Graphium podalirius* $\frac{3}{4}$ to $1\frac{1}{4}$ hr.; Lederer, 1938b
- G. marcellus* 1 hr.; Lederer, 1938b
- Papilio machaon* $\frac{1}{4}$ to $2\frac{3}{4}$ hr.; Lederer, 1938b
- Papilio zelicaon* 36 min. up to 30 hr. if male mated recently; Shields, 1967; Lawrece Gilbert, unpublished
- Papilio xuthulus* 10 min.; Lederer, 1938b
- Papilio* spp. more than 10 min. and less than 3 hr.; Clarke & Sheppard, 1956
- Aporia crataegi* several hr.; Lederer, 1938b
- Pieris napi* 50 min. to 3 hr. depending on temperature, rarely 5 days at low temperature; Petersen & Tenow, 1954
- Pieris brassicae* 1 hr., up to 3.5 hr. at low temperature; David & Gardiner, 1961
- Pieris rapae* 80 min.; Obara, 1967
- Pieris* spp. 1-4 hr., rarely 1-2 days; Lederer, 1938b
- Pontia daplidice* 30 min.; Lederer, 1938b
- Euchloe hyantis* occasionally overnight; P. Opler, written communication
- Euchloe ausonides* 30 min.; Scott, this study
- Anthocharis* spp. $\frac{1}{4}$ to 4 hr., rarely to next morning; Lederer, 1938b
- Colias eurytheme* about 1 hr., Burns, 1970
- Colias eurytheme* X *interior* 67 min.; Burns, 1970
- Colias* (seven species) $\frac{1}{2}$ to $3\frac{1}{2}$ hr., most 2-3 hr., one 5 hr.; Lederer, 1941
- Gonepteryx rhamni* 1-3 hr., one case more than 28 hr.; Lederer, 1938a
- **Danaus gilippus* 100 min. to 12 hr., usually several hr.; Burns, 1970
- Hipparchia semele* 45 min. to 2 hr.; Tinbergen et al. 1942
- **Neominois ridingsi* average 15 min.; Scott, this study
- **Poladyras minuta arachne* average 35 min., range 15-82 min. ($N = 27$) lasted 9 hr. and 11 hr. when the male mated immediately prior to timed mating; Scott, this study
- Euphydryas editha* average 109 min. in field, average 61 min. and average 87 min. at 25°C in lab in two replicates, average 94 min. in lab if male recently mated, average 108 min. in lab if male mated twice before recently; Labine, 1966
- Chlosyne lacinia* about 45 min.; Drummond et al., 1970
- Limenitis camilla* 30 to 130 min., up to 5 hr. if temperature drops; Lederer, 1960
- Limenitis* spp. 45 min. to over 2 hr.; Platt, 1969
- **Aglais urticae* occasionally overnight; Poulton, 1904
- Precis coenia* average 33 min.; Scott, this study
- **Callophrys augustinus* 2-8 hr., usually 4-6 hr.; Powell, 1968
- **Nordmannia ilicis* 1 hr. or more; Fiori, 1957
- Poanes hobomok* average 38 min.; Burns, 1970
- Hesperia metea* 2 hr.; Shapiro, 1965
- Erynnis tristis* 61 min.; Shields, 1967
- **Agathymus* spp. 3-4 hr.; Roever, 1964
- Pieris protodice* frequently overnight; A. Shapiro, written communication

hardly be assumed that organs present in thousands of butterfly species are nonfunctional, yet we are faced with the presence or absence of the structures in closely related species. The random presence or absence and modifications of structure and placement of the organs are ideally suited for isolating mechanisms (see below). More studies are needed on the use of androconia.

Female pheromones probably occur in most species (Table 3). The evidence for pheromones consists of experiments in *Argynnis*, *Hypolimnas*, *Hypaurotis*, anatomical evidence in other species (Table 5), and field observations in the other species, including observations of males locating females hidden from sight, and differential behavior toward virgin or freshly mated females and older females, when no visual cues are given by the females to enable the male to discriminate. Clark (1926) described female odors of 54 species. The fact that in many species unreceptive females perform rejection dances while receptive females remain quiescent also argues for the presence of female pheromones, because in these species females give the male fewer visual cues if they are receptive than if unreceptive. The female can mate before the wings are expanded in many patrolling species (*Graphium marcellus*, Edwards, 1868; *Papilio rutulus*; *Parnassius phoebus*; *Pieris protodice*, Shapiro, 1970; *Colias philodice*, Stern and Smith, 1960; *Ascia monuste*, Nielsen, 1961; and *Heliconius*, Edwards, 1881); in most cases a patrolling male accidentally wanders within a few meters of the newly emerged female, and then detects the pheromone. The short distance in which these pheromones usually act may mean that in some species the male detects biochemical differences between the sexes or between young and old individuals rather than a specific chemical manufactured by the female for the purpose. In a few genera (*Precis*; *Heliconius* (Crane, 1955), young males also are somewhat attractive to other males, and in *Hypolimnas*, males possess the pheromone to about the same extent as the females (Stride, 1956). In most species, however, the pheromone seems limited to or greater in the female.

The anatomical source of female pheromones is shown in Table 2. In some species such as *Hypaurotis* and *Precis*, a female pheromone is behaviorally suspected, but there is no obvious source; general biochemical differences between the sexes may be utilized, or the glands may be small. The female pheromone sources are usually glands, which may be associated with hairlike setae, or hair-pencils similar to those of males (but

no species has similar organs in both sexes except for *Thymelicus lineola*, in which they are located differently and are only superficially similar). The glands are located almost always near the end of the abdomen, because the female usually keeps her wings motionless during courtship so that wing scales cannot become transmitted as well as those of males, and the male is almost always behind the female often with his head near her abdomen prior to joining.

Sound. Some butterflies produce sounds (male *Hamadryas*, Ross, 1963; *Megathymus* females, Scott, this study), but the function of these sounds is unknown; they may serve as intra-specific communication, because some butterflies hear (*Heliconius* and *Hamadryas*, Swihart, 1967a).

Prezygotic Isolating Mechanisms. Because few interspecific copulating pairs are found in nature, the visual and olfactory factors of courtship are probably very important as isolating mechanisms. Males can physically mate with females of very many species. So far, only color and odor have been shown to be important as isolating mechanisms. Because closely related species usually have similar courtship movements, these movements may not function as an isolating mechanism. In the *Papilio glaucus*-group, the color of the conspecific female is important for the initial approach by the male, and it is probable that pheromone of a conspecific female is needed for continued courtship (Brower, 1959). In *Pieris napi-bryoniae* complex courtship was a weak isolating mechanism, even though differences in female pheromones and coloration (but not the male pheromone) occurred (Petersen, 1952, 1954). *Danaus gilippus* male hair-pencils possess a pheromone which is effective only on female *D. gilippus* and not on female *D. plexippus* (Myers, 1968, 1970; Meinwald et al. 1969a, 1969b; Myers and Brower, 1969; Pliske and Eisner, 1969; Schneider and Seibt, 1969). Another Danaine, *Lycorea*, has male pheromones different from both *Danaus* (Meinwald et al. 1966). *Heliconius erato* and *H. melpomene* males are attracted to red, while *H. besckei* males are attracted to yellow (Emsley, 1970). *Colias philodice* and the related entity *eurytheme* have different male pheromones; newly emerged females are less selective than are older females (Orley Taylor, oral communication). Because females are mated at an earlier age at high density, amount of hybridization is probably greater at high density. In *Parnassius* and *Acraea*, in which there are many species of almost identical appearance, the absence of courtship seems to require

that species-specific pheromones are used, but no evidence is available. Mating of closely related species in different areas of the habitat, as in *Hesperia*, serves at least to reduce interference between species. Mating at different times of day would serve as an isolating mechanism, but I know of no very closely related species with non-overlapping mating times.

Copulating posture. Males of almost all butterflies grasp the female from a position slightly behind her by facing the same direction as the female and bending the abdomen right or left 180° to grasp her abdomen. Then the male moves laterally until both sexes face opposite directions. The male bends his abdomen right or left depending on his position; there are no known species which bend only one direction. In *Parnassius*, the male grasps the ventral part of the female's thorax with his legs and bends his abdomen toward her, or occasionally if a male is between the female's wings, both sexes twist their abdomens to form the same position. In *Ornithoptera brookeana*, the male somehow manages to grasp the female while she is dorsal to him (Skertchly, 1889).

Behavior during copulation. Apparently only in the Danaeinae is there a postnuptial flight (the male always carries the female a short distance). In other species the pair remain at the site of mating, where they may separately or both bask, or may fly if disturbed. If disturbed, the sex which carries the other is usually fixed within species (Table 4). In taxa in which only one sex carries the other, the active sex also positions itself above the other, positions its wings outside of those of the other (but in some species the wings do not overlap), and is more likely to walk during copulation. At the end of copulation in *Precis* the female kicks and turns until the male is broken off; then the male flies away. In *Papilio zelicaon*, the male initiates uncoupling (Shields, 1967). In *Poladryas*, the two individuals merely separate.

Duration of Copulation (Table 5) seems to be partly inherited and species-specific, and partly affected by temperature and prior mating by the male. In four species duration increases at lower temperatures; Petersen and Tenow (1954) even developed an equation for this relationship. In *Precis napi*, *Euphydryas editha*, *Poladryas*, and *Papilio zelicaon*, copulation lasts longer if the male mated in the previous two days. Increased duration just after prior copulation may partly explain the longer matings of *Danaus* spp. (Burns, 1970) and *Callophrys augustinus* (Powell, 1968), which mated frequently. Long copu-

TABLE 6. Number of matings per male

Can mate at least twice

- Papilio zelicaon*, Lawrence Gilbert, oral communication
- Papilio machaon*, Clarke & Sheppard, 1956
- Papilio glaucus*, Clarke & Sheppard, 1956
- Papilio dardanus*, Clarke & Sheppard, 1956
- Pieris rapae*, Shapiro, 1970
- Pieris napi*, Petersen & Tenow, 1954
- Precis coenia*, Scott, this study
- Gonepteryx rhamni*, Lederer, 1941

Can mate at least four times

- Limenitis camilla*, Lederer, 1960
- Danaus plexippus* (can also mate twice per day), Burns, 1970
- Euphydryas editha* (can mate on successive days), Labine, 1966
- Limenitis* spp. (mate most readily on alternate days), Platt, 1969
- Pieris brassicae* (sometimes twice per day), David & Gardiner, 1961
- Acraea encedon* (can mate on successive days), Owen, 1966

Can mate at least five times

- Poladryas minuta arachne* (can mate on successive days and twice per day), Scott, this study
- Colias eurytheme* (can mate on successive days), Stern & Smith, 1960
- Callophrys augustinus* (can mate on successive days), Powell, 1968
- Papilio eurymedon* (can mate on successive days), Clarke & Sheppard, 1957

Can mate at least ten times

- Heliconius* sp., Lawrence Gilbert, oral communication

Can mate at least 13 times

- Pieris protodice*, Arthur Shapiro, written communication

lation in *Parnassius* may be needed to deposit the sphragis, a large structure deposited by the male preventing further mating. Species which mate only during part of the day might be expected to have shorter copulations, but this does not occur (Table 5). It is unlikely that copulation is prolonged until the female loses receptivity to other males, because in *Euphydryas editha* females reject males immediately after mating due to the presence of the spermatophore (Labine, 1966), and in the moth *Attveva punctella*, presence of the spermatophore itself caused short-term unreceptivity to males (Taylor, 1967).

Number of matings per male. The data available suggest that males can mate on successive days, and up to five times (rarely 13 times) per male, although males may mate more readily on alternate days (Table 6). Males which produce a large sphragis or large spermatophores probably mate less often due to depletion of the accessory glands.

Number of matings per female. In contrast to males which show little difference in mating frequency between species, the number of matings per female varies greatly between species (Table 7). Extremes are *Parnassius*, which never mates more than once, and *Danaus gilippus*, which can mate up to ten times. In the multiple mating species, number of matings depends on age (*Euchloe ausonides*, *Pieris brassicae*, *Colias philodice*, *Precis coenia*, *Hesperia pahaska*, *Amblyscirtes simius*, and *Ochlodes snowi*); only in *Hypaurotis* is this relationship weak. In *Pieris brassicae* the effective period between matings is six to nine days.

A sphragis is known in Acraeinae (*Planema*, *Acraea*, *Actinote*), Danainae (*Amauris*), and Papilionidae (*Parnassius*, *Thais*, *Luehdorfa*, *Eurycus*, *Cressida*, *Papilio plutonius*, *P. priabus*, and *Euryades*) (Eltringham, 1912; Lederer, 1938b). Males of these species probably mate less frequently than males of other species because males of *Parnassius* use the accessory gland fluid to form the sphragis (Eltringham, 1925) so several matings would deplete the glands. Owen & Chanter (1969), however, found that *Acraea encedon* males mate up to four times. In *Acraea thalia* males, the male has a hair pencil similar to *Danaus gilippus* which becomes almost completely incorporated into the sphragis (Eltringham, 1912); if these hairpencils are used in courtship as seems likely, the male would be able to mate only once or twice.

In all the species with a large sphragis, many similarities exist, including the absence of courtship, powerful odor of adults

TABLE 7. Average number of matings per mated female. Because number of matings depends on age in multiple-mating species, some of these averages may be too low. Number of matings per old female would be a better measure, but this was determined only by me. *—perching species. ?—may be a perching species. Others patrolling.

<i>Parnassius phoebus</i>	1.00	Scott, this study
<i>Parnassius clodius</i>	1.00	Shields, 1967
<i>Acraea</i> spp.	1.00	Eltringham, 1912
* <i>Lycaena arota</i>	1.02	Scott, this study
* <i>Poladryas arachne</i>	1.03	Scott, this study
* <i>Neominois ridingsii</i>	1.03	Scott, this study
* <i>Polites sabuleti</i>	1.03	Shields, 1967
<i>Heliconius erato</i> almost always once		Crane, 1955
? <i>Pseudocopaeodes eunus</i>	1.04	Shields, 1967
<i>Cercyonis pegala</i>	1.04	Burns, 1968
<i>Speyeria cybele</i>	1.05	Burns, 1968
? <i>Poanes viator</i>	1.06	Burns, 1968
* <i>Limenitis camilla</i> sometimes twice		Lederer, 1960
* <i>Atalopede campestris</i>	1.07	Burns, 1968
<i>Speyeria callippe</i>	1.08	Shields, 1967
? <i>Thymelicus lineola</i>	1.09	Burns, 1968
<i>Anthocaris sara</i>	1.09	Shields, 1967
* <i>Lycaena xanthoides</i>	1.10	Scott, this study
? <i>Wallengrenia otho</i>	1.13	Burns, 1968
<i>Coenonympha tullia</i>	1.15	Shields, 1967
* <i>Hesperia pahaska</i>	1.15	Scott, this study
* <i>Amblyscirtes simius</i>	1.15	Scott, this study
* <i>Precis coenia</i>	1.17	Scott, this study
<i>Chlosyne acastus</i>	1.19	Shields, 1967
<i>Papilio zelicaon</i>	1.24	Shields, 1967
<i>Colias philodice eurytheme</i>	1.30	Stern & Smith, 1960
<i>Euchloe ausonides</i>	1.32	Scott, this study
<i>Hypaurotis crysalus</i>	1.33	Scott, this study
* <i>Polites mystic</i>	1.33	Burns, 1968
<i>Erebia epipsodea</i> usually once, up to 3 times		Brussard & Ehrlich, 1970
* <i>Hesperia sassacus</i>	1.34	Burns, 1968
<i>Euphydryas editha</i> often twice, up to 3 times or more		Labine, 1964
* <i>Epargyreus clarus</i>	1.44	Burns, 1968
* <i>Euphyes vestris</i>	1.45	Burns, 1968
* <i>Ochlodes snowi</i>	1.65	Scott, this study
<i>Battus philenor</i>	1.73	Burns, 1968
<i>Papilio glaucus</i>	1.73	Burns, 1968
? <i>Lerema accius</i>	2.03	Burns, 1968
<i>Pieris brassicae</i> (10 days old)	2.30	David & Gardiner, 1961
<i>Pieris protodice</i> more than once often		Shapiro, 1970
<i>Danaus gilippus</i>	2.63	both <i>Danaus</i> from Burns, 1968
<i>Danaus plexippus</i> sometimes 2 times per days, up to 4 times at least		
<i>Pieris rapae</i>	2.66	Burns, 1968

of both sexes, and strong attraction of males to virgins. The male captures the female without any courtship in *Acraea*, *Planema* (Eltringham, 1912), and *Parnassius*. *Parnassius* and *Acraea* and probably most of the above have a female pheromone. Eltringham (1912) suggests that the large sphragis serves to inhibit the emission of the female pheromone in *Acraea*. In *Parnassius*, recently mated females are still attractive, but older mated females are not, so the same result is achieved as in *Acraea*. Other species of butterflies have a small plug in the copulatory orifice (Melitaeinae, some Hesperinae, and others) but the plug is often ineffective in preventing multiple mating, and courtship occurs.

Because males which plug the female will fertilize all her eggs, individuals of that genotype will increase in the population, even though this may reduce the viability of the population by reducing the number of recombinations. Capture of the female may be selected for because the male can always tell whether the female is virgin or mated by physically detecting the sphragis (or because of pheromone); if he detects that she is virgin, he can then mate immediately without wasting time courting. In other butterflies, determining the receptivity of the female may not be so easy, and one function of courtship is to increase the female's receptivity so that mating can occur. Capture may occur in *Parnassius* because the male must assume the venter-to-venter position in order to deposit the sphragis, which requires positioning the male using the legs. *Parnassius* and *Acraea* contain many species of similar appearance, so that the absence of courtship and female movement before copulation seems to require species-specific pheromones to prevent interspecific mating. The fate of sperm in the female is important; in most species sperm from the last mating fertilizes all the eggs (see below) which implies that males of all species would benefit genetically from "capture" of the female, and that the above factors rather than physiology must explain lack of courtship. The use of a sphragis may be rare because of energetic demands on the male.

Fertilization by different matings. Sperm from the last mating almost always fertilizes all the eggs laid by a female after that mating and until the next mating. This was shown in butterflies in *Papilio bianor* and *P. maackii* (Ae, 1962); *Papilio machaon*-group and *P. dardanus* (Clarke & Sheppard, 1962); *Euphydryas editha* (Labine, 1964); *Pieris rapae* (Shapiro, 1970). In moths, Taylor (1967) showed the phenomenon in *Atteva punctella*.

Significance of multiple mating. Mating with a non-virgin female is advantageous to the male (but less so than mating with a virgin) because all the female's subsequent eggs will be fertilized by him. Multiple mating is advantageous to the female to counteract previous infertile matings. In species with large spermatophores, I believe multiple mating also serves a nutritive function, perhaps permitting more eggs to be laid; in the moth *Galleria* digestion by proteolytic enzymes is completed by ten days (Chapman, 1969). A spermatophore may occupy a tenth or a fifth of the abdominal volume, and older spermatophores shrink until only remnants and the persistent "neck" remain, so that most of the spermatophore is absorbed and contributes to metabolism. Multiple mating may equalize sexual selection on both sexes by making the variance of number of matings per individual more similar in the two sexes; in species in which most females mate only once, the variance of number of matings per male will be much greater than in females so sexual selection will act more strongly on males. Color might be subject to sexual selection, but there seems to be no correlation of color or sexual dimorphism with frequency of mating (Table 7). Since females often mate near the site of emergence, females which mate only once will contribute more gene flow after immigration than females which mate again after emigration (Labine, 1964). However, species in which most females mate only once have a greater probability of genetic drift, since a smaller number of recombinations will occur than in species which can mate many times. These two forces oppose each other.

SUMMARY

There is tremendous diversity of wing, antenna, and body movements during courtship. Females can mate on the day of emergence, but males do not mate for several days. Visual factors important during courtship include movement, size, and general color. Unreceptive mated females reject males by a variety of stereotyped flight patterns (rejection dances) or stationary body postures (rejection postures) and occasionally by use of a repellent pheromone. Pheromones are common in both sexes and are used primarily as aphrodisiacs within a meter of the recipient. Male pheromones are generally produced on the wings, legs, or rarely on the end of the abdomen, while

female pheromones generally are produced on the end of the abdomen. Color and odor are important as isolating mechanisms. Males generally grasp the female to mate by bending the abdomen 180° laterally. Only one sex flies if a copulating pair is disturbed in most taxa; in a few taxa either sex may fly. Copulation lasts about ½ to 3 hours depending on the species, occasionally overnight (rarely 5 days). Copulation is longer at lower temperature and if the male recently mated. Males can mate five times or more, whereas number of matings per female varies greatly between species from only once to an average of three. A large sphragis, which prevents multiple female mating, is associated with lack of courtship and presumed pheromones of virgin females. The last mating usually fertilizes all subsequent eggs in multiple-mating females. Multiple mating serves a nutritive function in providing extra protein for oogenesis, it counteracts previous infertile matings, and it lessens the amount of gene flow after dispersal of the female.

LITERATURE CITED

- ABBOTT, W. 1959. Local Autecology and behavior in *Pieris protodice* Boisduval and Leconte with some comparisons in *Colias eurytheme* Boisduval (Lepidoptera: Pieridae). *Wasmann Jour. Biol.* 17: 279-297.
- AE, S. A. 1962. Some problems in hybrids between *Papilio bianor* and *P. maackii*. *Academia* (Nanzan Univ., Japan). 33: 21-8.
- BARTH, R. 1944. Die Männlichen Duftorgane einiger *Argynnis*-Arten. *Zool. Jb.* Anat. 68: 331-362.
- . 1952. Die Hautdrüsen Des Männchens von *Opsiphanes invirae isagoras* Fruhst (Lepidoptera, Brassolidae). *Zool. Jahrb. Abt. Anat. Ontog. Tiere.* 72: 216.
- . 1959. Phylogenetische Betrachtungen der Duftapparate einiger Nymphalinae (Lepidoptera, Nymphalidae). *Academia Brasileira de Ciencias.* 31: 557-565.
- . 1960. Männliche Duftorgane Brasilianischer Lepidopteren. 23. Mitteilung Vergleichende Betrachtung der Duftschnappen verschiedener Pieriden. *Anais da Academia Brasileira de Ciencias.* 32: 281-298.
- BROWER, L. P. 1959. Speciation in butterflies of the *Papilio glaucus* group. II. Ecological relationships and interspecific sexual behavior. *Evolution.* 13: 212-228.
- , J. V. Z. BROWER, and F. P. CRANSTON. 1965. Courtship behavior of the queen butterfly, *Danaus gilippus berenice* (Cramer). *Zoologica.* 50: 1-39.
- BRUSSARD, P. F., and P. R. EHRLICH. 1970. Adult behavior and population structure in *Erebia epipsodea* (Lepidoptera, Satyrinae). *Ecology.* 51: 880-885.
- BURNS, J. M. 1964. Evolution in skipper butterflies of the genus *Erynnis*. *Univ. Calif. Pub. Ent.* 37: 1-214.
- . 1968. Mating frequency in natural populations of skippers and butterflies as determined by spermatophore counts. *Proc. Nat. Acad. Sci.* 61: 852-859.
- . 1970. Duration of copulation in *Poanes hobomok* and some broader speculations. *Psyche.* 77: 127-130.

- CHAPMAN, R. F. 1969. The insects. Structure and function. The English Univ. Press, London. 819 pp.
- CLARK, A. H. 1926. Fragrant butterflies. *Smithsonian Inst. Annual Report*.
- CLARKE, C. A., and P. M. SHEPPARD. 1956. Hand-pairing of butterflies. *Jour. Lepid. Soc.* 10: 47-53.
- . 1957. The breeding in captivity of the hybrid *Papilio glaucus* female X *P. eurymedon* male. *Lepid. News*, 11: 201-205.
- . 1962. Offspring from double matings in swallowtail butterflies. *Entomologist*, 95: 199-203.
- CRANE, JOCELYN. 1955. Imaginal behavior of a Trinidad butterfly, *Heliconius erato hydara* Hewitson, with special reference to the social use of color. *Zoologica*, 40: 167-196.
- . 1957. Imaginal behavior in butterflies of the family Heliconiidae: changing social patterns and irrelevant actions. *Zoologica*, 42: 135-145.
- DAVID, W. A. L., and B. O. C. Gardiner. 1961. The mating behavior of *Pieris brassicae* (L.) in a laboratory culture. *Bull. Ent. Res.* 52: 263-80.
- DIXEY, F. A. 1932. The plume scales of the Pierinae. *Trans. Ent. Soc. London*, 80: 57-75.
- DRUMMOND, B. A., G. L. BUSH, T. C. EMMEL. 1970. The biology and laboratory culture of *Chlosyne lacinia* Geyer (Nymphalidae). *Jour. Lepid. Soc.* 24: 135.
- EDWARDS, W. H. 1881. On certain habits of *Heliconius charitonius* L., a species of butterfly found in Florida. *Papilio*, 1: 209-215.
- . 1868-1897. The butterflies of North America. 3 vols. Published by the author.
- ELTRINGHAM, H. 1912. A monograph of the African species of the genus *Acraea* Fab., with a supplement on those of the Oriental region. *Trans. Roy. Ent. Soc. London*, 1912: 1-374.
- . 1919. Butterfly vision. *Trans. Ent. Soc. London*, 67: 1-49.
- . 1925. On the source of the sphragidial fluid in *Parnassius apollo* (Lepidoptera). *Trans. Roy. Ent. Soc. London*, 1925: 11-15.
- EMMEL, T. C. 1972. Mate selection and balanced polymorphism in the tropical nymphalid butterfly, *Anartia fatima*. *Evolution*, 26: 96-107.
- EMSLEY, M. G. 1970. An observation on the use of color for species-recognition in *Heliconius besckei* (Lepidoptera, Nymphalidae). *Journ. Lepid. Soc.* 24:25.
- EVANS, W. H. 1952. Luring *Anthocaris reakti* into the net. *Journ. Lepid. Soc.* 6:100.
- FIORI, G. 1957. *Strymon ilicis* Esp. (Lepidoptera, Lycaenidae). *Boll. Ist. Ent. Univ. Bologna*, 22:205-256.
- FREILING, H. H. 1909. Duftorgane der Weiblichen Schmetterlinge nebst Beiträgen zur Kenntnis der Sinnesorgane auf dem Schmetterlingsflügel. *Z. Wiss. Zool.* 92:210-291.
- GOTZ, B. 1951. Die Sexualduftstoffe an Lepidopteren. *Experientia*, Basle, 7:406-418.
- ILLIG, K. G. 1902. Duftorgane der männlichen Schmetterlinge. *Zoologica* (Stuttgart), 15:34 pages.
- KAMES, P. 1966. Bau und Wirkungsweise der Duftorgane von Schmetterlingen. *Entomol. Berichte, Berlin*, 1966:37-44.
- LABINE, P. A. 1964. Population biology of the butterfly *Euphydryas editha*. I. Barriers to multiple inseminations. *Evolution*, 18:335-336.
- . 1966. The reproductive biology of the checkerspot butterfly, *Euphydryas editha*. PhD thesis, Stanford University.
- LEDERER, G. 1938a. Zur Fortpflanzungsbiologie (Paarung) der *Gonepteryx*-Arten (Lepidoptera). *Verh. 7 Int. Congr. Ent.* 2:808-813.
- . 1938b. Die Naturgeschichte der Tagfalter. Teil I. Handbuch für den praktischen Entomologen. Band II: Tagfalter. Otto Wrede, Frankfurt.
- . 1941. Die Naturgeschichte der Tagfalter. Teil II. Handbuch für den praktischen Entomologen. Band II: Tagfalter. Alfred Kernen, Stuttgart.

- . 1960. Verhaltensweisen der Imagines und der Entwicklungsstadien von *Limenitis camilla camilla* L. (Lepidoptera, Nymphalidae). *Zeit. fur Tierpsychologie*. 17:521-546.
- LONGSTAFF, G. B. 1912. Butterfly-hunting in many lands. Longmans, Green and Co., London. 729 p.
- MAGNUS, D. B. 1950. Beobachtungen zur Balz und Eiablage des Kaisermantels *Argynnis paphia* L. (Lepidoptera, Nymphalidae). *Z. Tierpsychol.* 7:435-449.
- . 1954. Experimentelle Untersuchungen am Kaisermantel zur Analyse optischer Auslösungsreize. *Verh. Dtsch. Ent. Tag.* Hamburg. 1953: 58-75.
- MAGNUS, D. B. 1958. Experimental analysis of some "overoptimal" stimuli in the mating behavior of the fritillary butterfly *Argynnis paphia* L. (Lepidoptera, Nymphalidae). *Proc. Tenth Int. Congr. Ent. Montreal*. 2:405-418.
- . 1963. Sex-limited mimicry II. Visual selection in the mate choice of butterflies. *16th Int. Congr. Zool.* 4:179-183.
- MALICKY, H. 1961. Über die Ökologie von *Lycaeides idas* L., insbesondere über seine Symbiose mit Ameisen. *Z. Arbeit. Ost. Ent.* 13: 33-49.
- MARSHALL, G. A. K. 1901. On the female pouch in *Acraea*. *Entomologist*. 34:73-75.
- MASTERS, J. H., and J. T. SORENSSEN. 1969. Field observations on forest *Oeneis*. *Journ. Lepid. Soc.* 23: 155-161.
- McCUBBIN, C. 1971. Australian Butterflies. Nelson, Melbourne. 206 p.
- MEINWALD, J., A. M. CHALMERS, T. E. PLISKE, and T. EISNER. 1969b. Identification and synthesis of trans trans-3-7-di methyl-2-6-deca dien-1-10-dioic acid, a component of the pheromonal secretion of the male monarch butterfly. *Journ. Chem. Soc. D. Chem. Common.* 3:86-87.
- . Y. C. MEINWALD, and P. H. MAZZOCCHI. 1969a. Sex pheromone of the queen butterfly: chemistry. *Science*. 164:1174-1175.
- . Y. C. MEINWALD, J. W. WHEELER, T. EISNER, and L. P. BROWER. 1966. Major components in the exocrine secretion of a male butterfly (*Lycorea*). *Science*. 151:583-585.
- MYERS, J. 1968. The structure of the antennae of the Florida queen butterfly, *Danaus gilippus berenice* (Cramer). *Journ. Morphol.* 125:315-328.
- . 1970. Olfaction in the Florida queen butterfly—honey odor receptors. *Journ. Insect Physiol.* 16:573-578.
- . and L. P. BROWER. 1969. A behavioral analysis of the courtship pheromone of the queen butterfly, *Danaus gilippus berenice* (Lepidoptera, Danaidae). *Journ. Insect Physiol.* 15:2117-2130.
- NIELSEN, E. T. 1961. On the habits of the migratory butterfly *Ascia monuste* L. *Biol. Medd. Dansk. Vid. Selskab.* 23:1-81.
- OBARA, Y. 1967. Mating behavior—butterflies. Seibutsu Kagaku (Japan Sci. Rev.) 18:67-73.
- . 1970. Studies on the mating behavior of the white cabbage butterfly, *Pieris rapae crucivora* Boisduval (Lepidoptera, Pieridae). III. Near ultraviolet reflection as the signal for intraspecific communication. *Z. Vergl. Physiol.* 69:99-116.
- OLIVER, C. G. 1972. Genetic and phenotypic differentiation and geographic distance in four species of lepidoptera. *Evolution*. 26:221-241.
- OWEN, D. F. 1966. Predominantly female populations of an African butterfly. *Heredity*. 21:443-451.
- OWEN, D. F., and D. O. CHANTER. 1969. Population biology of tropical African butterflies. Sex ratio and genetic variation in *Acraea encedon* (Lepidoptera, Nymphalidae). *Journ. Zool. London*. 157:345-375.

- PETERSEN, B. 1952. The relations between *Pieris napi* L. and *Pieris bryoniae* Ochs. *Trans IX Int. Congr. Ent.* 1:83-87.
- . 1954. Geographische variation von *Pieris (napi) bryoniae* durch bastardierung mit *Pieris napi*. *Uppsala Universitet—Zoologiska Bidrag.* 30: 355-397.
- , and O. TENOW. 1954. Studien am Rapsweissling und Bergweissling (*Pieris napi* L. und *Pieris bryoniae* O.). Isolation und Paarungsbiologie. *Zool. Bidrag Fran Uppsala.* 30:169-198.
- , O. TORNBLOM, and N. O. BODIN. 1952. Verhaltensstudien am Rapsweissling und Berkweissling (*Pieris napi* L. und *Pieris bryoniae* Ochs.). *Behavior.* 4:67-84.
- PHIPPS, J. 1968. Pupation and emergence in *Phalanta phalanta aethiopica* (Roth. & Jordan) (Lepidoptera, Nymphalidae) in Nigeria. *Proc. Roy. Ent. Soc. London A.* 43:80-84.
- PLATT, A. P. 1969. A simple technique for hand-pairing *Limenitis* butterflies (Nymphalidae). *Journ. Lepid. Soc.* 23:109-112.
- PLISKE, T. E., and T. EISNER. 1969. Sex pheromone of the queen butterfly, *Danaus gilippus berenice*. *Science.* 164:1170-1172.
- POULTON, E. B. 1904. No title (oviposition and courtship of *Aglais urticae*). *Proc. Roy. Ent. Soc. Lond.* 1 June, p. xli.
- . 1912. The anal tufts of *Glutaphrissa saba* extended in courtship. *Proc. Roy. Ent. Soc. Lond.* 7 Feb. p. v.
- . 1918. No title (mating of African butterflies). *Proc. Ent. Soc. London*, 5 June, p. lxxxviii.
- POWELL, J. A. 1968. A study of area occupation and mating behavior in *Incisalia irioides* (Lepidoptera, Lycaenidae). *Journ. New York Ent. Soc.* 76:47-57.
- PRIDDLE, T. R. 1960. In: Urquhart, F. 1960. The monarch butterfly. *Univ. Toronto Press.* (pp. 152-156).
- ROER, H. 1959. Über Flug und Wandergewohnheiten von *Pieris brassicae* L. *Zeit. Ang. Ent.*, Hamburg. 44: 272-309.
- ROEVER, K. 1964. Bionomics of *Agathymus* (Megathymidae). *Journ. Res. Lepid.* 3:103-120.
- ROSS, G. N. 1963. Evidence for lack of territoriality in two species of *Hamadryas* (Nymphalidae). *Journ. Res. Lepid.* 2: 241-246.
- RUTKOWSKI, F. 1971. Notes on some south Florida lepidoptera. *J. Lepid. Soc.* 25: 137-139.
- SCHNEIDER, D., and U. SEIBT. 1969. Sex pheromone of the queen butterfly: electroantennogram responses. *Science.* 164: 1173-1174.
- SHAPIRO, A. M. 1965. Ecological and behavioral notes on *Hesperia metea* and *Atrytonopsis hianna*. *Journ. Lepid. Soc.* 19:215-221.
- . 1970. The role of sexual behavior in density-related dispersal of pierid butterflies. *Amer. Nat.* 104:367-372.
- SHIELDS, O. 1967. Hilltopping. *Journ. Res. Lepid.* 6:69-178.
- , & J. EMMEL. 1973. Carrying-pair behavior of butterflies. *J. Res. Lepid.* in press.
- SKERTCHLY, S. B. J. 1889. On the habits of certain Bornean butterflies. *Ann. and Mag. Nat. Hist.* 6:209.
- STELLWAAG, F. 1924. Der Baumweissling *Aporia crataegi* L. *Zeit. fur Angew. Ent.* 10:273-312.
- STERN, V. M., and R. F. SMITH. 1960. Factors affecting egg production and oviposition in populations of *Colias philodice eurytheme* Boisduval (Lepidoptera, Pieridae). *Hilgardia.* 29:411-454.
- STRIDE, G. O. 1956. On the courtship behavior of *Hypolimnys misippus* L. (Lepidoptera, Nymphalidae), with notes on the mimetic association with *Danaus chrysippus* L. (Lepidoptera, Danaidae). *British Journ. Anim. Behav.* 4:52-68.

- . 1957. Investigations into the courtship behavior of the male of *Hypolimnys misippus* L. (Lepidoptera, Nymphalidae), with special reference to the role of visual stimuli. *British Journ. Anim. Behav.* 5:153-167.
- . 1958a. On the courtship behavior of a tropical mimetic butterfly, *Hypolimnys misippus* L. (Nymphalidae). *Proc. X Int. Congr. Ent. Montreal* 2:419-24.
- . 1958b. Further studies on the courtship behavior of African mimetic butterflies. *Anim. Behav.* 6:224-230.
- SWIHART, S. L. 1967a. Hearing in butterflies (Nymphalidae: *Heliconius*, *Ageronia*). *Journ. Insect Physiol.* 13:469-476.
- . 1967b. Neural adaptations in the visual pathway of certain Heliconiine butterflies, and related forms, to variations in wing coloration. *Zoologica*. 52:1-14.
- TAYLOR, O. R. 1967. Relationship of multiple mating to fertility in *Atteva punctella* (Lepidoptera; Yponomeutidae). *Entom. Soc. Amer. Ann.* 60:583-590.
- TEMPLE, V. 1953. Some notes on the courtship of butterflies in Britain. *Entom. Gazette*. 4:141-161.
- TINBERGEN, N., B. J. D. MEEUSE, L. K. BOEREMA, W. W. VARIOS-SEAU. 1942. Die Balz des Samtfalters, *Eumenis* (*Satyrus*) *semele* (L.). *Z. Tierpsychol.* 5:182-226.
- URBAHN, E. 1913. Abdominale Duftorgane bei weiblichen Schmetterlingen. *Jena. Z. Naturwiss.* 59:277.
- WARREN, B. C. S. 1936. Monograph of the genus *Erebia*. London. 407 p.
- WHEELER, G. 1915. The carrying habits of the sexes in paired butterflies. *Entomologist's Record*. 28: 204.